Received: 13 November 2019 | Revised: 25 August 2020 | Accepted: 4 November 2020

DOI: 10.1111/csp2.328

CONTRIBUTED PAPER

Conservation Science and Practice — A journal of the Society for Conservation Biology — Open Access

WILEY

Top predator ecology and conservation: Lesson from jaguars in southeastern Mexico

Carlos Cruz[1,2] | **Heliot Zarza**[3] | **Javier Vidal-Mateo**[2] | **Vicente Urios**[2] | **Gerardo Ceballos**[1]

[1]Laboratorio de Ecología y Conservación de Fauna Silvestre, Instituto de Ecología, Universidad Nacional Autónoma de México, Coyoacan, Mexico

[2]Grupo de investigación Zoología de Vertebrados, Universidad de Alicante, Alicante, Spain

[3]Departamento de Ciencias Ambientales. Lerma de Villada, Universidad Autónoma Metropolitana - Unidad Lerma, CBS, Lerma, Mexico

Correspondence

Gerardo Ceballos, Laboratorio de Ecología y Conservación de Fauna Silvestre, Instituto de Ecología, Universidad Nacional Autónoma de México, TCiudad Universitaria, UNAM, Coyoacan 04510, Ciudad de México, Mexico.
Email: gceballo@ecologia.unam.mx

Funding information

Alianza WWF-Telmex-Telcel; World Wildlife Fund

Abstract

Our research is the most comprehensive study of jaguar behavior ecology in Mexico. By analyzing and describing the movements and use of the space, as well as the interactions among individual jaguars, we can better understand their behavioral differences, habitat use, and home range. This type of information is critical for the development and implementation of effective and appropriate conservation strategies. We identified home range size for 14 jaguars in a 13-year period and described the interspecific relations and use of space by the percentages of overlap of the territories between individuals. Collectively, the average home range size was larger than 200 km^2, ranging from 48 to 633 km^2 and averaging 296 km^2 for males varied and 37–435 km^2, with an average of 148 km^2, for females. However, home range sizes did not differ significantly among males or females. Male territory overlapped about 3.3% on average (range 2.5–15.5%), suggesting that most of the time males avoid each other. Average overlap of female territory was 12%, ranging from 7 to 100%. Males share an average of 18% (range 2–56%) of its territory and with up to five females, suggesting that a given male may be related to all of them at certain periods of time. There were no seasonal changes (dry and rainy seasons) in home range sizes for both male and females. Our research is an important contribution to the ecological information essential for landscape-level conservation plans for the protection of the jaguars and the biological diversity of the wider Yucatan Peninsula in which they inhabit.

KEYWORDS

activity patterns, animal movements, conservation, habitat fragmentation, home range, jaguar, movement ecology

1 | INTRODUCTION

Human activities are responsible for the catastrophic decline in populations and extinction of thousands of animal and plant species throughout the world, and the current rates of loss, unprecedented in recent geologic time, are evidence we have entered the sixth mass extinction (Barnosky et al., 2011; Ceballos et al., 2015). Habitat loss and degradation, primarily the result of rapid human population growth, and its associated impacts, are the main drivers of the loss of wildlife in general, and of carnivores, in particular (Cardillo et al., 2004; Di Minin et al., 2016; Laurance, 2006; Ripple et al., 2014). Climate change will further exacerbate the stress on biodiversity in general and predators in particular (e.g., Ceballos et al., 2015; Ripple et al., 2014).

The wide array and intensity of threats carnivores have experienced during the last century have substantially reduced the size of their populations and distribution ranges (Angerbjorn et al., 2013; Cardillo et al., 2004; Ceballos et al., 2015; Di Minin et al., 2016; Medellín, de la Torre, Zarza, Chávez, & Ceballos, 2016). Despite their decreased numbers, large carnivores still exert important effects on the stability of ecosystems and the structure of trophic networks (Ripple et al., 2014). Their movement through the landscape, driven by processes that act on different temporal and spatial scales, and plays a fundamental role in the structure and dynamics of populations, communities, and ecosystems, as well as in the biodiversity and its evolution (Nathan et al., 2008).

Large carnivores require extensive areas to maintain viable populations, and the primary factors that determine the use of space are the animal's size, metabolic demands, prey availability, sociality, hunting tactics, habitat suitability, and interactions with other species (Ripple et al., 2014). For large cats, such as tigers and leopards, patterns of spatial distribution are partly determined by prey density, distance from human habitation, forest type, topography, and water courses (Carroll & Miquelle, 2006; Simcharoen et al., 2014). Interactions with other species are also important determinants of spatial distribution (de la Torre, Núñez, & Medellín, 2017a) for tropical cats as jaguars (*Panthera onca*) and pumas (*Puma concolor*).

Jaguars, the largest felid in the neotropics, range from northern Mexico to northern Argentina (Quigley et al., 2017). According to de la Torre, González-Maya, Zarza, Ceballos, and Medellín (2017), jaguars are extant in 18 countries throughout the Americas with the exception of El Salvador and Uruguay, and are functionally extinct in the United States of America. Although the historic distribution range of the jaguar extended over 8,420,000 km^2, almost half (42%) has been lost in the last century and, outside the Amazonian region., the population has declined by 82%. Major current threats are hunting, habitat loss and fragmentation, and prey population decline.

Currently in Mexico jaguars live in large forested areas along the Pacific coastal plain, in the western Sierra Madre, and the Gulf of Mexico coastal plain, all the way to the southeastern reaches of the Yucatan Peninsula (Chávez, Zarza, de la Torre, Medellín, & Ceballos, 2016). Jaguars are likely to be key species for maintaining ecosystem function and services in their distribution range (de la Torre & Medellín, 2011; Miller et al., 2001), and in areas where they are still abundant they play a key role in trophic cascades and prey regulation (Cavalcanti & Gese, 2009; Terborgh et al., 2001). However, its current distribution range has contracted between 48 and 55% of the historical value in the last century (de la Torre, González-Maya, et al., 2017; Sanderson et al., 2002) and their populations have experienced a severe decline since the 20th century (de la Torre, Núñez, & Medellín, 2017b; Medellín et al., 2016; Quigley et al., 2017; Roques et al., 2014; Saavedra-Mendoza, Cun, Horstman, Carabajo, & Alava, 2017; Sanderson et al., 2002). Habitat loss and fragmentation driven primarily by agriculture and cattle ranching encroachment, hunting, prey depletion, disease introduced by domestic animals, and human-jaguar conflicts are the main threats Ceballos, Zarza, Chávez, & González-Maya, 2016; De la Torre et al., 2017b; Medellín et al., 2016; Rodríguez-Soto et al., 2011; Saavedra-Mendoza et al., 2017).

Accurate assessment of their home range and an understanding of their behavior as it relates to their movement would provide critical information on jaguar ecology (Morato et al., 2016) and guidance for conservation-oriented landscape management (Carroll & Miquelle, 2006; 2012; Ordiz, Bischof, & Swenson, 2013; Simcharoen, Barlow, Simcharoen, & Smith, 2008). Previous research on the spatial ecology of jaguars has generated important information about their movements and behavior. Home ranges are variable along the gradient of their latitudinal distribution, between climate seasons, and between sexes (Cavalcanti & Gese, 2009; de la Torre et al., 2017a; McBride & Thompson, 2018; Morato et al., 2016; Núñez, Miller, & Lindzey, 2002). In Paraguay, Brazil and Argentina, home ranges varied from 37 to 1,268 km^2 for males and 25 to 718 km^2 for females (Cavalcanti & Gese, 2009; McBride & Thompson, 2018; Morato et al., 2016). In Mexico, home ranges in the tropical rain forest are on average 431 km^2 for males and 181 km^2 for females (de la Torre et al., 2017b) but only 25 km^2 in the dry season and 65 km^2 in the wet season for females in the tropical dry forests (Núñez et al., 2002). However, estimates of home range and population densities in many studies are based on sample sizes of very few animals. For example, only two jaguars were recorded in a study of Ecuador′s mainland coast jaguar population (Saavedra-Mendoza et al., 2017).

Our research is based the largest number of jaguars sampled in Mexico, and there are only two other studies that have larger samples, 44 in Brazil (Morato et al., 2001) and 26 in Bolivia (Maffei, Cuéllar, & Noss, 2004). We analyze the movement of 14 jaguars to address the following questions: (i) What is home range size of males and females; (ii) What does the home range overlap reveal about the social structure of jaguars? (iii) Are there seasonal variations in home ranges? (iv) What are the conservation implications of this information?

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area focused on the Calakmul region of the Yucatan Peninsula in southern Mexico and included portions of the states of Campeche and Quintana Roo (Figure 1). This region consists of extensive tropical forests and supports a mosaic of human-dominated land uses such as agriculture, cattle grazing, and forestry (Briceño-Méndez et al., 2017). Approximately 1,300,000 ha of tropical forest are included the federal protected Calakmul Biosphere Reserve and the Campeche state protected areas of Balam Kú and Balam Kin (Chávez, Ceballos, & Amín, 2007). The extensive forest areas outside those reserves belong to local communities (known as "ejidos") and are used for forestry, and in some instances, conservation activities (González-Abraham, Schmook, & Calmé, 2007).

The dominant plant communities are tropical subperennial forest, deciduous forest, and seasonally flooded forests (Martínez & Galindo-Leal, 2002). The area has a subhumid tropical climate with summer rains, annual temperature of 24.6°C, and average annual total rainfall between 1,000 and 1,300 mm (Instituto Nacional de Estadística y Geografía (INEGI), 2017). Much of the region has a karst-type topography (Martínez & Galindo-Leal, 2002) which causes rainwater to seep rapidly underground, but there are some permanent water bodies, locally known as "aguadas" (Reyna-Hurtado et al., 2010). However, during the wet season (June–November) the region is partially flooded. The Calakmul region has a high biological diversity, including almost 80% of the plant species registered in the Yucatan Peninsula, 350 species of birds and almost 100 species of mammals (Secretaría de Medio Ambiente, Recursos Naturales y Pesca (SEMARNAP), 2000). The Calakmul region has the largest population of jaguars in Mexico, and together with the adjacent Guatemalan and Belizean forests, the largest such population north of the Orinoco River (Ceballos, Chávez, Rivera, Manterola, & Wall, 2002; Sanderson et al., 2002). Human settlements and agricultural operations occupy approximately 24% of the Yucatan Peninsula (Chávez & Zarza, 2009), and continued encroachment of agriculture and cattle ranching in the Yucatan Peninsula in general, and in the Calakmul region in particular, has resulted in high deforestation rates that represent a serious threat to conservation efforts (Ávila-Nájera, Chávez, Lazcano-Barrero, Pérez-Elizalde, & Alcántara-Carbajal, 2015).

We conducted our fieldwork in three localities: Costa Maya (18°13′15.08″ N; 89°30′15.34" W), located

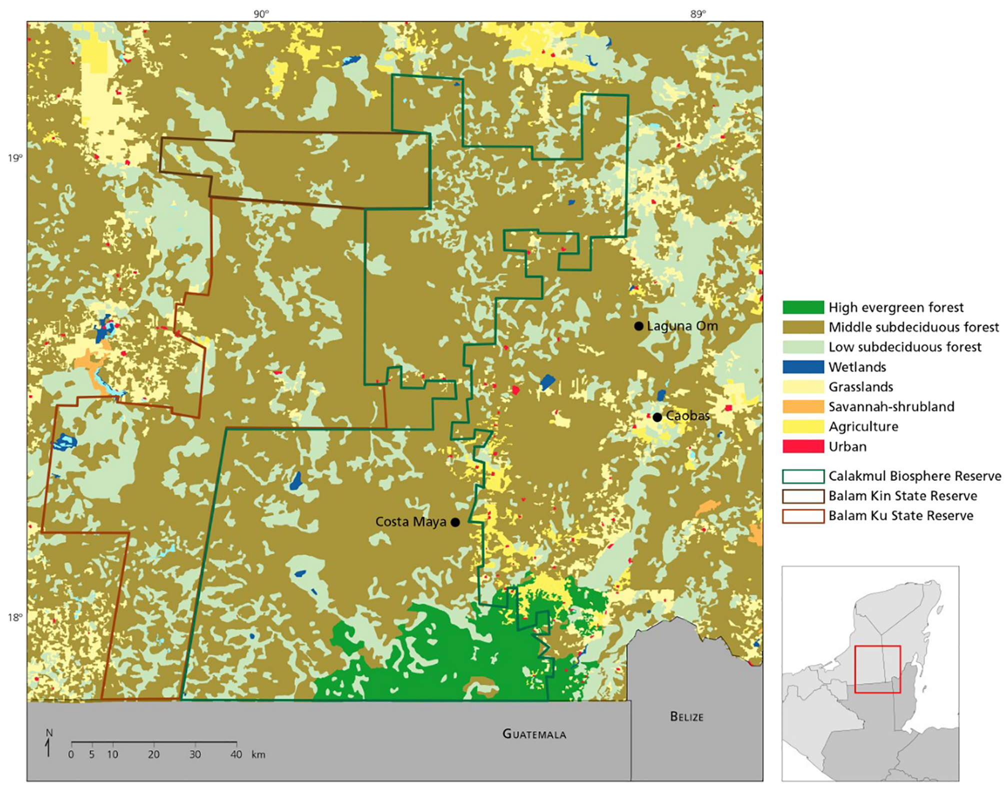

FIGURE 1 Study area in the southern Yucatan Peninsula include the localities of: Costa Maya (18° 13′ 15.08″ N, 89° 30′ 15.34″ W); Caobas (18° 24′ 12.61″ N, 88° 59′ 57.28″ W); and Laguna Om (18°37′59″ N, 89°05′39″ W)

in the southern part of the Calakmul Biosphere Reserve in the state of Campeche and contiguous with large areas of tropical forests (Figure 1); and the localities of Caobas (18°24′12.61″ N; 88°59′57.28″ W) and Laguna Om (18°37′59″ N, 89°05′39″ W), which are forestry management areas in the state of Quintana Roo, located in the zone of influence of the Calakmul Biosphere Reserve, and adjacent to a mosaic of forests, cattle, and agricultural lands (Briceño-Méndez et al., 2017).

TABLE 1 Estimates of the minimum convex polygon (MCP) and home range size using the 95, 75, and 50% fixed kernels of the jaguars captured and tracked

Jaguar ID	Sex	Localities	Period tracked	Total number of locations	Minimum convex polygon (MCP)	Home range		
						Fixed kernel 95%	Fixed kernel 75%	Fixed kernel 50%
Tony	♂	Costa Maya	Jun 2002–May 2003	611	975.674	633.443	171.686	38.830
Sandra	♀	Costa Maya	May 2009–Sep 2009	1,289	71.368	49.171	16.439	4.583
Ulises	♂	Costa Maya	Apr 2009–Oct 2009	5,322	321.590	185.966	38.295	9.065
José	♂	Costa Maya	Apr 2009–Oct 2009	5,064	229.766	90.534	18.427	3.865
Guillermo	♂	Costa Maya	Apr 2009–Oct 2009	4,423	60.462	48.891	13.921	2.503
Paola	♀	Caobas	Apr 2001–Jan 2002	226	74.012	37.275	6.581	2.361
Eugenia	♀	Caobas	Jun 2001–Mar 2003	318	295.807	278.959	69.748	20.982
Dalia	♀	Caobas	Feb 2003–Mar 2009	1,239	755.206	435.772	124.411	32.508
Patricia	♀	Caobas	Mar 2003–Feb 2004	77	194.619	83.356	38.640	20.026
Lico	♂	Caobas	Apr 2005–May 2006	295	534.039	519.560	129.824	34.761
Verónica	♀	Caobas	Apr 2005–Mar 2009	190	102.705	106.671	59.114	14.236
Melisa	♀	Caobas	Mar 2005–Feb 2006	73	116.508	80.126	16.055	2.260
630,187	♀	Laguna Om	May 2013–May 2014	1774	166.387	133.167	21.660	2.009
UNK54	♀	—	Apr 2008–Mar 2009	245	154.182	130.183	45.688	11.867
Mean				—	289.452	200.934	55.035	14.275

TABLE 2 Number of locations, estimates of the minimum convex polygon (MCP) and home range size using the 95, 75, and 50% fixed kernels for the wet and dry season

Jaguar ID	Sex	Total number of locations	Wet season				Dry season			
			Fixed kernel 95%	Fixed kernel 75%	Fixed kernel 50%	MCP	Fixed kernel 95%	Fixed kernel 75%	Fixed kernel 50%	MCP
Tony	♂	611	582.005	147.268	35.171	595.677	728.694	229.304	85.037	851.400
Sandra	♀	1,289	49.171	16.439	4.583	71.368	—	—	—	—
Ulises	♂	5,322	185.966	38.295	9.065	321.590	—	—	—	—
José	♂	5,064	90.534	18.427	3.865	229.766	—	—	—	—
Guillermo	♂	4,423	48.891	13.921	2.503	60.462	—	—	—	—
Paola	♀	226	20.814	4.794	1.767	44.526	73.020	16.248	6.965	72.270
Eugenia	♀	318	348.239	146.433	39.177	295.807	114.821	21.765	5.411	171.059
Dalia	♀	1,239	517.835	186.646	69.113	689.448	373.450	82.317	35.260	543.537
Patricia	♀	77	45.061	13.350	3.906	25.469	94.834	53.994	30.458	167.831
Lico	♂	295	400.891	84.626	30.012	510.126	—	—	—	—
Verónica	♀	190	105.351	42.045	5.647	101.194	82.668	46.795	16.841	51.811
Melisa	♀	73	52.419	6.573	2.123	80.429	96.651	42.421	5.250	108.793
630,187	♀	1,774	149.105	61.666	18.282	153.650	59.125	7.489	2.565	116.868
UNK54	♀	245	91.144	39.473	5.595	101.701	149.500	40.627	11.335	134.194

2.2 | Data collection

Over the duration of the 13 years of field research (2001–2014) we used trained hounds to help locate and tree or corner adult jaguars, a technique successfully employed in other research projects (Crawshaw & Quigley, 1991; Hoogesteijn, Hoogesteijn, & Mondolfi, 1992; Morato et al., 2001). Once located, we immobilized the specimen using a combination of 0.06 mg/kg of Medetomidine 20 mg/mL (Medised 20×) and 5–6 mg/kg of Ketamine 200 mg/mL (Ketanil) dispensed through a 1 or 3 cc aluminium pneu-dart discharged by a Dan-inject CO_2 rifle (model I.M); Atimil (20 mg/mL) was used as the antagonist.

We followed ethical and security standards required by the General Wildlife Office during the capture and handling procedures (see permits and animal sampling certification in Supporting Information). While immobilized, we recorded standard metrics including body measurements and weight, rectal temperature, heart and respiratory rate, reproductive state, parasites presence and sex, and attached GPS collars (Telonics® TGW-5477) to facilitate tracking their movements once they were released. The collars were programmed to send location data every 2–4 hr using the ARGOS system.

2.3 | Home range estimation and analysis

We recorded a total of 17,438 location data points during a minimum 6-month period for all of the 14 jaguars (nine females and five males) to describe their home range, including size, location, movement patterns, and their interactions with other jaguars. We grouped home ranges into different categories to identify and describe habitat

TABLE 3 Social structure of the tracked jaguars: relations between females and males, percentage of shared territory, and intersection area are presented

Sex	Jaguar ID	Related with female	Shared territory (%)	Intersection area (km^2)	Related with male	Shared territory (%)	Intersection area (km^2)
Females	Dalia	Verónica	20.34	88.63	Lico	67.61	294.64
		Eugenia	39.93	174.03			
		Paola	8.47	36.92			
		Melissa	7.48	32.60			
	Verónica	Dalia	83.11	88.63	Lico	44.65	47.64
		UNK54	29.74	31.73			
	UNK54	Verónica	25.37	31.73	Lico	12.13	16.04
		Melissa	13.03	16.96			
	Eugenia	Paola	100	—	Lico	37.59	104.87
		Dalia	62.38	174.03			
	Paola	Eugenia	13.36	—	Lico	34.97	13.04
		Dalia	99.05	36.92			
	Melisa	UNK54	21.17	16.96	—	—	—
		Dalia	40.69	32.60			
	Sandra	—	—	—	Tony	18.85	9.27
Males	Ulises	—	—	—	José	2.5	4.65
					Guillermo	4.09	7.61
	José	—	—	—	Ulises	5.13	4.65
	Guillermo	—	—	—	Ulises	15.57	7.61
	Tony	Sandra	1.46	9.27	—	—	—
	Lico	Paola	2.51	13.04	—	—	—
		Eugenia	20.18	104.87			
		Dalia	56.7	294.64			
		Verónica	9.17	47.64			
		UNK54	3.09	16.04			

use and interactions between individuals and linked their behavior to ecological and spatiotemporal variables. We evaluated home range size in both wet and dry seasons, compared range characteristics for males with those of females, and described differences in habitat use where same sex and opposite sex overlap occurred. While this study does not identify causal factors that drive spatial dynamics or jaguar density, it provides data on the movement patterns and insights into important space-related intraspecific relationships.

To estimate the home range size for each animal, we used the Animal Movement Extension for ArcView 3.2 (Hooge & Eichenlaub, 1997) with the 95, 75, and 50% fixed kernel method (Worton, 1989) and the least squares cross-validation procedure to calculate the smoothing parameter H (Silverman, 2018). In our calculation of the fixed kernels to evaluate differences in range size, we standardized the tracking period by using only the first 6 months of data collected for each individual. However, we used the whole dataset available for each period and for each animal to assess differences in home ranges between the dry (December–May) and wet (June–November) seasons.

We used the 95% kernel as a representative area and a maximum period of 3 years of shared territory to calculate the percentage of home range overlap where it occurred for the different individuals. This time frame was selected based on the age of the individuals and assumption they may have used the territory in which other jaguars were present in the same space and during the same time period. We differentiated the overlap between males and females, between different males and between different females. Differences in home range size between sexes and seasons were evaluated using Students t-test and the Mann–Whitney U-tests (if data were non-normal). All statistical analyses (including statistical measures) were performed with IBM SPSS Statistics ver. 22.0. Significance level was established at p <.05 and the results are presented as mean ± standard deviation (SD).

3 | RESULTS

3.1 | Home range size

The average size of home range for all individuals was larger than 200 km^2 (95% kernel, Table 1). Although the home range of the males was on average larger than that of females (Tables 1 and 2), the difference was not significant for any of the measures used (95% kernel: $U = 15.0$, $p = .317$; 75% kernel: $t = 0.709$, $p = .507$; 50% kernel:,

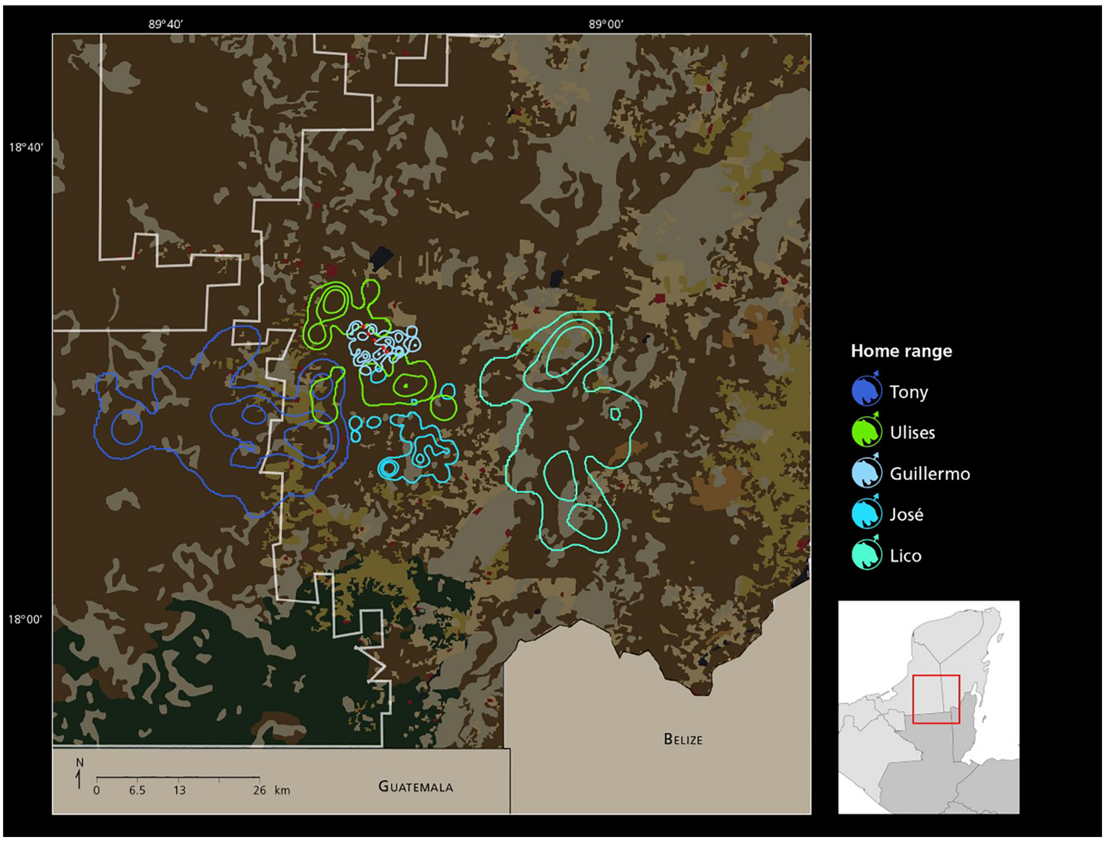

FIGURE 2 Home range (95, 75, and 50% kernels) for the five male jaguars tracked by GPS telemetry in southeastern Mexico. Male territories have very little or no overlap with other males

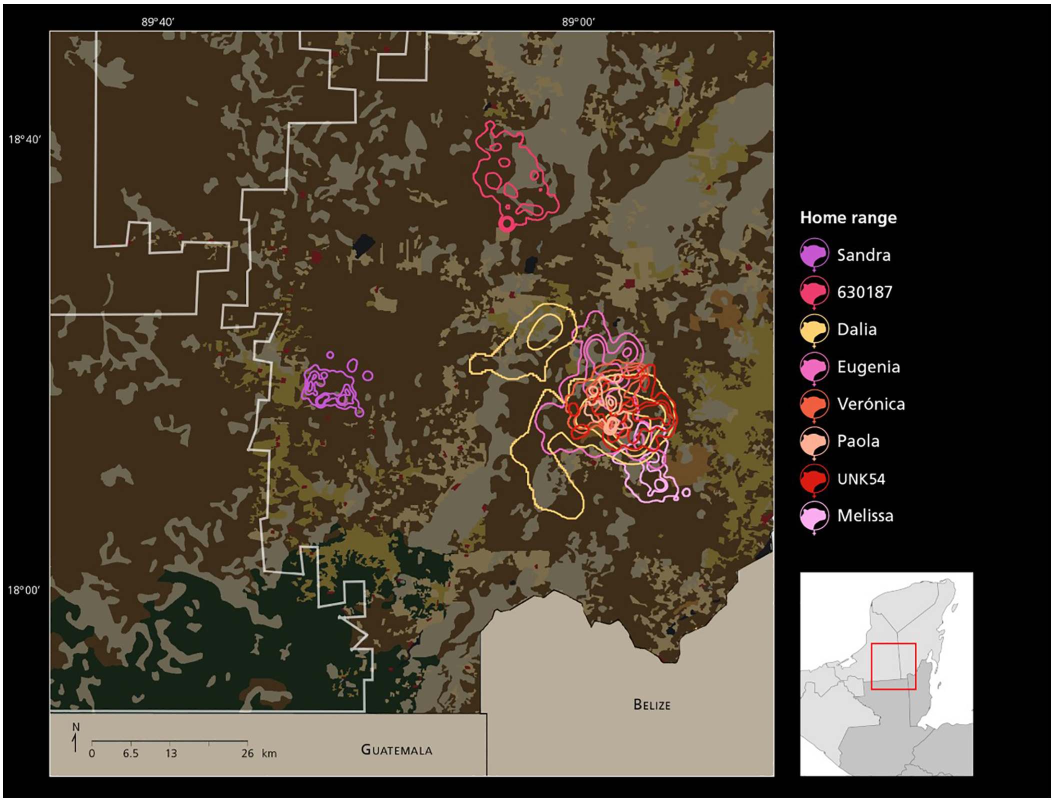

FIGURE 3 Home range (95, 75, and 50% kernels) of the nine female jaguars tracked by GPS telemetry in southeastern Mexico. There is a large overlap of female home ranges

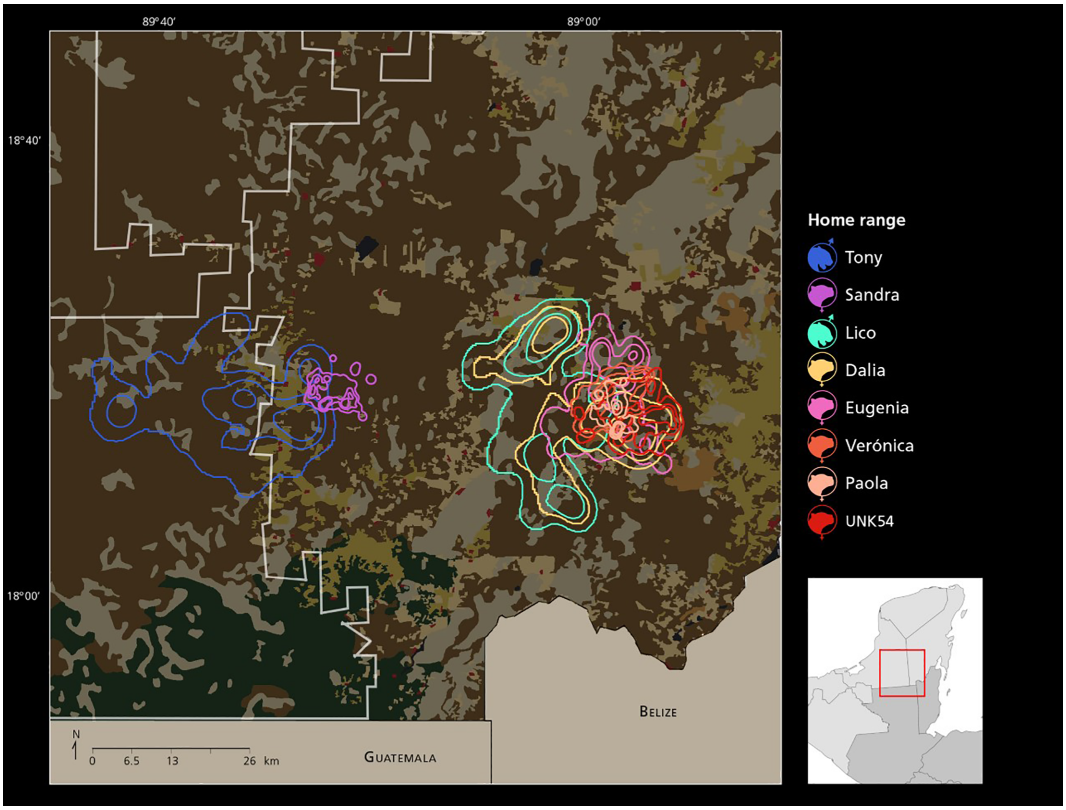

FIGURE 4 Overlap of home range (95, 75, and 50% kernels) between males and females, including Tony (male) with Sandra (female), and Lico (male) with five females: Paola, Eugenia, Dalia, Veronica, and UNK54

$t = 0.477$, $p = .642$; MCP: $t = 2.001$, $p = .069$). The home range of males was extremely variable, ranging from roughly 49–633 km^2 and averaged 296 km^2 (Table 1); for females, it ranged from 37 and 436 km^2 and averaged of 148 km^2 (Table 1). Although we did not expect it, home range sizes for both sexes were did not vary much between the rainy and dry season (Table 2) (95% kernel: $U = 55.0$, $p = .643$; 75% kernel: $U = 55.0$, $p = .644$; 50% kernel: $U = 48.0$, $p = .369$; MCP: $U = 57.0$, $p = .734$). For example, male home ranges were roughly 192 km^2 on average during the wet season and 196.9 km^2 during the dry season (95% kernel). The mean 95% kernel home range size for male jaguars during wet season was 261.66 and 728.64 km^2 during the dry season, but this value was obtained for only one male during this season. Among females, mean home range size was 153.24 km^2 in the wet season and 130.51 km^2 in the dry season.

3.2 | Social structure

There was a notable difference in the percentage of range overlap between males and females. The very small amount of overlap among male jaguars (average of 3.3% and range 2.5–15.5%) suggests that males avoid each other most of the time (Table 3, Figure 2). In contrast, the home range of females overlapped an average of 12% of the territory (range 7–100%; Table 3). The home range of two females, named Paola and Eugenia, overlapped completely. At the other extreme, the overlap of two other females, Dalia and Melisa, was only 7.5% of the range (Figure 3).

Male and female home range overlap averaged 18% (range 2–56%; Table 3), and our data showed a male can share his territory with up to five females (Figure 4), suggesting it can be associated with all the females that share the overlap areas during specific time periods. Among the 14 animals analyzed, the specimen identified as "630,187" was the only female that did not overlap her home range and was not associated to any of the other jaguars tagged in this study. All specimens were considered adults because of their age (at least 2 years old) and dispersal from mother (Baker, Deem, Hunt, Munson, & Johnson, 2002), and therefore our analysis of range overlap was limited to this age group.

4 | DISCUSSION

The tracking data we obtained by satellite radio telemetry provided detailed information on jaguar movements, use of the space and interactions between individuals and contributes to our understanding of their ecological needs as well as individual behavioral differences (Colchero et al., 2011). This information is critical in developing conservation strategies necessary to protect them and their range.

4.1 | Home ranges

Previous research demonstrated variability in movement behavior among some same-species herbivores and carnivores (e.g., lions, polar bears, and wolves; Morato et al., 2016), and these individual differences may be influenced by environmental conditions (Singh et al., 2012). While our study also showed variability between individuals in size of range, (37–436 km^2 for females; 49–633 km^2 for males) it also revealed that the range tended to be somewhat larger than that cited in a previous study of jaguars (10–125 km^2 for females; 25–625 km^2 for males) in the Lacandona Rainforest, Calakmul and Chamela-Cuixmala, Mexico (Chávez, 2009; de la Torre et al., 2017b).

Jaguars are well adapted to the flooded ground and rainy conditions that occur throughout much of its range (Crawshaw & Quigley, 1991). Our data did not show any seasonal (wet and dry) differences in home range size and boundaries even in the flooded low areas of the tropical subperennial forests. The relatively flat topography of the southern Yucatan Peninsula supports a homogeneous distribution of prey populations throughout the year, and therefore jaguars of this area do not need to modify their home range or hunting strategies. We also did not identify any shift in home range during the dry season even though it corresponded with increased human activity and disturbances, including regulated hunting. In contrast to our observations, Núñez et al. (2002) noted larger home range areas during the rainy season, but the ultra-high frequency (UHF) tracking, based on triangulation, is less robust and precise compared to the satellite-based tracking method we used. Likewise, Crawshaw and Quigley (1991) noted that the wet season flooding in the northern part of Brazil's Pantanal is a major ecological influence and the majority of terrestrial vertebrates, including the jaguar and its prey, drastically reduce their home range and foraging areas.

Although the tropical subperennial forest may flood in low areas, the relatively flat topography of southern Yucatan Peninsula supports a homogeneous distribution of prey populations. We observed that jaguars appear adapted the flooded ground and rainy conditions common in most of its Yucatan range (Crawshaw & Quigley, 1991) and do not modify their home range size. We also noted that hunting activities by humans in the study area are not a major impact on jaguar home range.

4.2 | Social structure

Like the behavior of many large felids except for the lion, male jaguars maintain their territory with minimal overlap (Cavalcanti & Gese, 2009; Ordiz et al., 2013), especially as it relates to other males. The largest portion of shared territory for two males (15.57%; Table 3) involves the home range of jaguar "Guillermo" which separates two equally large territories occupied by jaguar "Ulises." In one instance, "Ulises" traverses the 6.62 km (measured in a straight line) through "Guillermo's" home range in a period of only 3 hr and 10 min (Figure 5). The home range of males depends on food availability and optimization of reproductive potential with receptive females that may be constrained by their metabolic limits (McBride & Thompson, 2018; Morato et al., 2016). The significant difference in the size of each male's home range appears to be independent of the monitoring time and probably reflects a characteristic of jaguars as a species, quality of the habitat, and the capacity to occupy larger territories.

The median size of home range for females was smaller compared to male home ranges, but this difference was not significant (Table 1). This trend of smaller size has been noted by other research in the Mayan Forests of southern Mexico and Guatemala (de la Torre, González-Maya, et al., 2017; de la Torre et al., 2017a) and in Paraguay (McBride & Thompson, 2018). As with the males, there was a high degree of variability in home ranges size. However, unlike male jaguars and other large felids such as tigers which have minimal overlap of about 3–4% (Simcharoen et al., 2014) as a strategy to guarantee access to the best prey for raising young individuals in the dispersal stage, female jaguars tended to have a larger overlap of home range. At least one pair, "Eugenia" and "Paola," shared 100% of their home range (Table 3). Female jaguars seek an optimal minimum space for their home range to maximize potential food availability and reproductive success while minimizing metabolic costs (McBride & Thompson, 2018).

Likewise, by analyzing the territorial behavior of males and females, our data, which show that males share their home range simultaneously with several females (Figures 4 and 6; Table 3), is consistent with studies in Bolivia (Maffei et al., 2004), Brazil (Cavalcanti & Gese, 2009) and southern Mexico and Guatemala (de la Torre et al., 2017a). In one outstanding example of mutual use of space, male jaguar "Lico" shares about 8.33% of his home range with each of five females (Figure 4). The percentage of home range female shares with "Lico," however, is much larger because the female range is smaller than that of the male and is embedded in, or at least partially surrounded by, a male's home range.

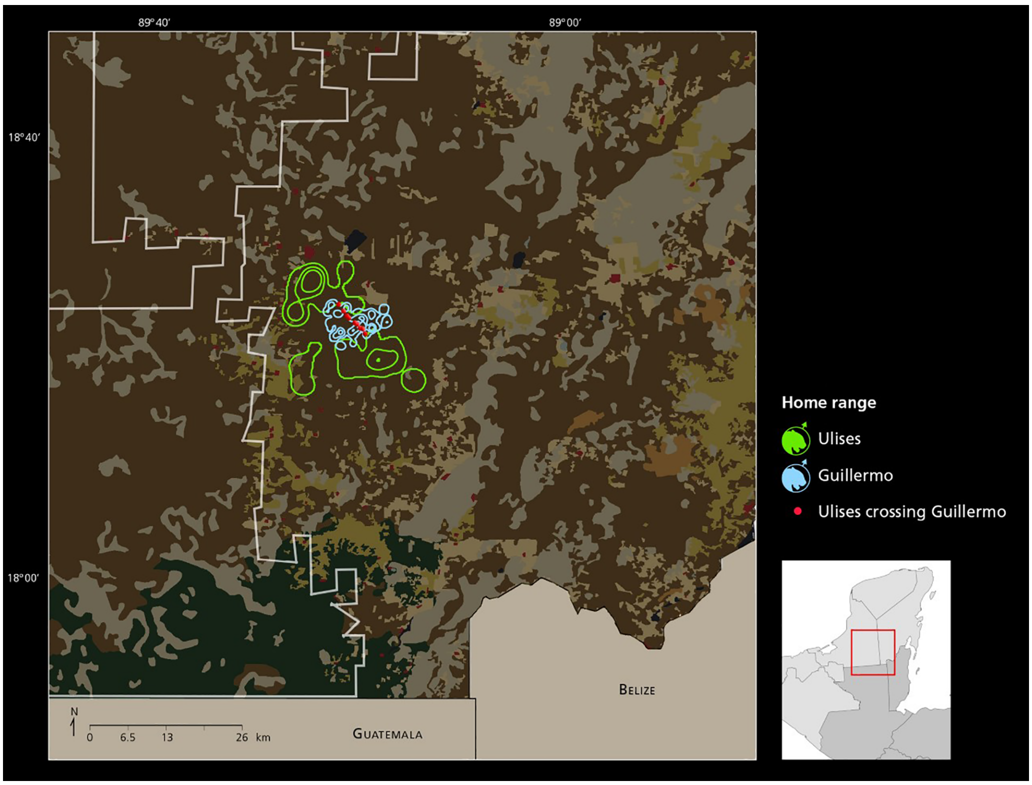

FIGURE 5 Home range (95, 75, and 50% kernels) of two male jaguars (Guillermo and Ulises) showing an almost complete exclusion between them. The red dots show the path of Ulises crossing the territory of Guillermo (6.62 km in 3 hr. 10 min)

The portion of the male and female overlapping home ranges suggests the range is extensive and the spatial distribution is controlled by reproductive males whose territories do not overlap with that of other males. The home range of males is likely to overlap with the home range of several potential reproductive partners and large enough to protect against predation of the young by other males (de la Torre et al., 2017a).

4.3 | Implications for conservation

Our study revealed important information about jaguar ecology and behavior that will help in their management and conservation strategies and programs in the Yucatan Peninsula and southern Mexico, generally. The current population of about 2,000 jaguars in the Yucatan Peninsula in Mexico is the largest in a region that extends into Central America (Ceballos et al., 2016; Ceballos et al., in press), and conservation efforts there are pivotal to ensuring the stability of their population and the ecological services they provide.

Landscape-level conservation strategies are needed to conserve jaguar populations. However, currently protected natural areas in the Yucatan Peninsula are discontinuous, and while most regions are still connected with corridors of forests and other natural ecosystems, these areas often lack official protection against deforestation (Ceballos et al., 2016; Ceballos et al., 2018). Together with other research, our study suggests that a major effort must be initiated to expand the size of the protected areas such as the Calakmul Biosphere Reserve, create additional protected areas, and design and protect biological corridors (see also Ceballos et al., 2016, 2018). Based on the results we presented here and the Mexico jaguar census data (Ceballos et al., in press), we are promoting a doubling of the size of the Calakmul Biosphere Reserve to 1.4 million hectares, which will make it the largest tropical reserve in Mexico and Central America, and the creation of jaguar biological corridors in the Peninsula to maintain population connectivity. Such a concerted focus on conservation of umbrella species such as jaguars may be the most effective and immediately strategy to improve future conservation prospects for much of the terrestrial ecosystems in the Yucatan Peninsula.

ACKNOWLEDGMENTS

The authors would like to thank the Alianza WWF - Fundacion Telmex/Telcel, the Universidad Nacional Autonoma de Mexico (project DGAPA, PAPIT IN208017), Amigos de Calakmul A.C., and the BBVA Foundation Award for the Conservation of Biodiversity (2017) for funding and support for this project. These financing sources had no participation in the data interpretation or in the document edition for publication. The authors also thank the ejidos Costa Maya, Caobas, Laguna Om, and the Calakmul Biosphere Reserve for allowing them to carry out the study in their lands. The authors would also like to thank Sara Morollón for the helpful revision of the manuscript. This manuscript is part the requirements of the PhD in Applied Zoology of the University of Alicante of Carlos Antonio Cruz González.

CONFLICT OF INTEREST

The authors have no financial or other conflicts of interest to report.

AUTHOR CONTRIBUTIONS

Gerardo Ceballos designed the study, collected the data, and wrote the manuscript; Heliot Zarza collected the data; Carlos Cruz led the organization of the manuscript, organize the data, and wrote the manuscript; Javier Vidal and Vicente Urios organized and analyzed the data, and made comments on the manuscript. All authors reviewed all drafts of the manuscript and gave their final approval for publication

DATA AVAILABILITY STATEMENT

Data used for this study belongs to the authors. Access to the data will be granted upon request.

ETHICS STATEMENT

Trapping and handling of the jaguars was done under several permits of the Mexican Natural Resources authorities.

ORCID

Carlos Cruz https://orcid.org/0000-0003-1091-1003
Gerardo Ceballos https://orcid.org/0000-0001-8374-2656

REFERENCES

Angerbjorn, A., Eide, N. E., Dalén, L., Elmhagen, B., Hellstrom, P., Ims, R. A., … Henttonen, H. (2013). Carnivore conservation in practice: Replicated management actions on a large spatial scale. *Journal of Applied Ecology*, *50*, 59–67.

Ávila-Nájera, D. M., Chávez, C., Lazcano-Barrero, M. A., Pérez-Elizalde, S., & Alcántara-Carbajal, J. L. (2015). Estimación poblacional y conservación de felinos (Carnivora: Felidae) en el norte de Quintana Roo, México. *Revista de Biología Tropical*, *63*, 799–813.

Baker, W., Deem, S., Hunt, A., Munson, L., & Johnson, S. (2002). Jaguar species survival plan. *Guidelines for Captive Management of Jaguars*, *1*, 9–13.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O., Swartz, B., Quental, T. B., … Mersey, B. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*(7336), 51–57.

Briceño-Méndez, M., Naranjo, E., Pérez-Irineo, G., Contreras-Perera, Y., Sandoval-Serés, E., & Hidalgo-Mihart, M. G. (2017).

Richness and trophic guilds of carnivorous mammals in Ejido Nuevo Becal, Calakmul, Campeche, Mexico. *Therya*, *8*, 145–150.

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., & Mace, G. M. (2004). Human population density and extinction risk in the world's carnivores. *PLoS Biology*, *2*(7), e197. https://doi.org/10.1371/journal.pbio.0020197

Carroll, C., & Miquelle, D. G. (2006). Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian Far East: The role of protected areas and landscape matrix in population persistence. *Journal of Applied Ecology*, *43*, 1056–1068.

Cavalcanti, S. M. C., & Gese, E. M. (2009). Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy*, *90*, 935–945.

Ceballos, G. (1989). In press. Beyond words: Jaguar population trends, conservation, and public policy in Mexico. PlosOne.

Ceballos, G., Chávez, C., Rivera, A., Manterola, C., & Wall, B. (2002). Tamaño poblacional y conservación del jaguar en la Reserva de la Biosfera Calakmul, Campeche, México. In R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, Jr., A. Rabinowitz, K. H. Redford, et al. (Eds.), *El jaguar en el nuevo milenio* (pp. 403–417). Mexico City, México: Fondo de Cultura Económica, Universidad Nacional Autónoma de México, Wildlife Conservation Society.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*, e1400253.

Ceballos, G., Zarza, H., Cerecedo, G., Lazcano, M. A., Huerta, M. A., De la Torre, A., & Morales, Y. R. J. J. (2018). *Corredores biológicos y áreas prioritarias para la conservación del jaguar en México*. México: ANCJ.

Ceballos, G., Zarza, H., Chávez, C., & González-Maya, J. F. (2016). Ecology and conservation of jaguars in Mexico. *Tropical Conservation: Perspectives on Local and Global Priorities*, *13*, 273.

Chávez, C. (2009). *Ecología poblacional y conservación de Jaguar (Panthera onca) y del puma (Puma concolor), en la region de Calakmul, y sus implicaciones para su conservacion en la Peninsula de Yucatan, México*. (Doctoral dissertation, Ph.D. Thesis). Universidad de Granada, España.

Chávez, C., Ceballos, G., & Amín, M. (2007). Ecología poblacional del jaguar y sus implicaciones para la conservación en la Península de Yucatán. In G. Ceballos, C. Chávez, R. List, & H. Zarza (Eds.), *Conservación y manejo del jaguar en México: Estudios de caso y perspectivas* (pp. 91–100). México: Conabio - Alianza WWF- Telcel – Universidad Nacional Autónoma de México city.

Chávez, C., & Zarza, H. (2009). Distribución potencial del hábitat del jaguar y áreas de conflicto humano-jaguar en la Península de Yucatán. *Revista Mexicana de Mastozoología*, *13*, 46–62.

Chávez, C., Zarza, H., de la Torre, J. A., Medellín, R. A., & Ceballos, G. (2016). Distribución y estado de conservación del jaguar en México. In R. A. Medellín, J. A. de la Torre, H. Zarza, C. Chávez, & G. Ceballos (Eds.), *El jaguar en el siglo XXI: la perspectiva continental* (pp. 112–136). Mexico City: Fondo de Cultura Económica, Universidad Nacional Autónoma de México.

Colchero, F., Conde, D. A., Manterola, C., Chávez, C., Rivera, A., & Ceballos, G. (2011). Jaguars on the move: Modeling movement to mitigate fragmentation from road expansion in the Mayan Forest. *Animal Conservation*, *14*, 158–166.

Crawshaw, P. G., & Quigley, H. B. (1991). Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology*, *223*, 357–370.

de la Torre, J. A., González-Maya, J. F., Zarza, H., Ceballos, G., & Medellín, R. A. (2017). The jaguar's spots are darker than they appear: Assessing the global conservation status of the jaguar *Panthera onca*. *Oryx*, *52*, 300–315.

de la Torre, J. A., & Medellín, R. (2011). Jaguars *Panthera onca* in the greater Lacandona ecosystem, Chiapas, Mexico: Population estimates and future prospects. *Fauna & Flora International, Oryx*, *45*, 546–553.

de la Torre, J. A., Núñez, J. M., & Medellín, R. A. (2017a). Spatial requirements of jaguars and pumas in southern Mexico. *Mammalian Biology*, *84*, 52–60.

de la Torre, J. A., Núñez, J. M., & Medellín, R. A. (2017b). Habitat availability and connectivity for jaguars (*Panthera onca*) in the southern Mayan Forest: Conservation priorities for a fragmented landscape. *Biological Conservation*, *206*, 270–282.

Di Minin, E., Slotow, R., Hunter, L. T. B., Montesino-Pouzols, F., Toivonen, T., Verburg, P. H., … Moilanen, A. (2016). Global priorities for national carnivore conservation under land use change. *Nature Scientific Reports*, *6*, 23814.

González-Abraham, A., Schmook, B., & Calmé, S. (2007). Distribución espaciotemporal de las actividades extractivas en los bosques del ejido Caoba, Quintana Roo. *Investigaciones Geográficas*, *62*, 69–86.

Hooge, P. N., & Eichenlaub, B. (1997). *Animal movement extension to ArcView. Version 1.1*. Anchorage, Alaska: Alaska Biological Science Center. US Geological Survey.

Hoogesteijn, R., Hoogesteijn, A., Mondolfi, E. (1992). *El dilema 'depredacion vs. conservacion' del jaguar y análisis de la mortalidad de bovinos causada por felinos en tres hatos del Llano Venezolano*. *Proceedings of the Symposium*: Felids of Venezuela: Biology, Ecology and Conservation. Caracas, pp. 129–169.

Instituto Nacional de Estadística y Geografía (INEGI). (2017). *Anuario estadístico y geográfico de Quintana Roo 2017*. México: Instituto Nacional de Estadística y Geografía Available from https://www.datatur.sectur.gob.mx/ITxEF_Docs/QROO_ANUARIO_PDF.pdf

Laurance, W. F. (2006). Have we overstated the tropical biodiversity crisis? *Trends in Ecology and Evolution*, *22*, 65–70.

Maffei, L., Cuéllar, E., & Noss, A. (2004). One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of Zoology*, *262*, 295–304.

Martínez, E., & Galindo-Leal, C. (2002). La vegetación de Calakmul, Campeche, México: Clasificación, descripción y distribución. *Boletin de la Sociedad Botánica de México*, *71*, 7–32.

McBride, R. T., & Thompson, J. J. (2018). Space use and movement of jaguar (*Panthera onca*) in western Paraguay. *Mammalia*, *82*, 540–549.

Medellín, R. A., de la Torre, J. A., Zarza, H., Chávez, C., & Ceballos, G. (2016). *El jaguar en el siglo XXI: La perspectiva continental*. Mexico City: Fondo de Cultura Económica, Universidad Nacional Autónoma de México.

Miller, B., Dugelby, B., Foreman, D., Martínez del Río, C., Noss, R., Phillips, M., … Willcox, L. (2001). The importance of large carnivores to healthy ecosystems. *Endangered Species Update*, *18*, 202–210.

Morato, R. G., Conforti, V. A., Azevedo, F. C., Jacomo, A. T., Silveira, L., Sana, D., … Barnabe, R. C. (2001). Comparative analyses of semen and endocrine characteristics of free-living versus captive jaguars (*Panthera onca*). *Reproduction*, *122*, 745–751.

Morato, R. G., Stabach, J. A., Fleming, C. H., Calabrese, J. M., De Paula, R. C., Ferraz, K. M., … Paviolo, A. (2016). Space use and movement of a neotropical top predator: The endangered jaguar. *PLoS One*, *11*, e0168176.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *PNAS*, *105*, 19052–19059.

Núñez, R., Miller, B., & Lindzey, F. (2002). Ecología del jaguar en la reserva de la biosfera Chamela-Cuixmala, Jalisco, México. In R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, Jr., A. Rabinowitz, K. H. Redford, et al. (Eds.), *El jaguar en el nuevo milenio* (pp. 107–125). Mexico City: Fondo de Cultura Económica, Universidad Nacional Autónoma de México, Wildlife Conservation Society.

Ordiz, A., Bischof, R., & Swenson, J. E. (2013). Saving large carnivores, but losing the apex predator? *Biological Conservation*, *168*, 128–133.

Quigley, H., Foster, R., Petracca, L., Payan, E., Salom, R., & Harmsen, B. (2017). *Panthera onca*. The IUCN Red List of Threatened Species. e. T15953A50658693.

Reyna-Hurtado, R., O'Farril, G., Sima, D., Andrade, M., Padilla, A., & Sosa, L. (2010). Las aguadas de Calakmul: Reservorios de vida silvestre y de la riqueza natural de México. CONABIO. *Biodiversitas*, *93*, 1–6.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., … Schmitz, O. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484.

Rodríguez-Soto, C., Monroy-Vilchis, O., Maiorano, L., Boitani, L., Faller, J. C., BrioneS, M. A., … Falcucci, A. (2011). Predicting potential distribution of the jaguar (*Panthera onca*) in Mexico: Identification of priority areas for conservation. *Diversity and Distributions*, *17*, 350–361.

Roques, S., Furtado, M., Jácomo, A. T. A., Silveira, L., Sollmann, R., Torres, N. M., … Palomares, F. (2014). Monitoring jaguar populations *Panthera onca* with non-invasive genetics: A pilot study in Brazilian ecosystems. *Oryx*, *48*, 361–369.

Saavedra-Mendoza, M., Cun, P., Horstman, E., Carabajo, S., & Alava, J. J. (2017). The last coastal jaguars of Ecuador: Ecology, conservation and management implications. In A. B. Shrivastav & K. P. Singh (Eds.), *Big cats* (pp. 1–21). Croatia: InTech.

Sanderson, E. W., Chetkiewicz, C. L., Medellín, R. A., Rabinowitz, A., Redford, K. H., Robinson, J. G., & Taber, A. B. (2002). Un análisis geográfico del estado de conservación y distribución de los jaguares a través de su área de distribución. In R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, Jr., A. Rabinowitz, K. H. Redford, et al. (Eds.), *El jaguar en el nuevo milenio* (pp. 551–600). Mexico City: Fondo de Cultura Económica, Universidad Nacional Autónoma de México, Wildlife Conservation Society.

Secretaría de Medio Ambiente, Recursos Naturales y Pesca (SEMARNAP). (2000). *Programa de manejo de la Reserva de la Biosfera de Calakmul. Secretaria del Medio Ambiente, Recursos Naturales y Pesca*. México, D.F.: Instituto Nacional de Ecología.

Silverman, B. W. (2018). *Density estimation for statistics and data analysis*. London: Chapman and Hall/CRC.

Simcharoen, A., Savini, T., Gale, G. A., Simcharoen, S., Duangchantrasiri, S., Pakpien, S., & Smith, J. L. D. (2014). Female tiger *Panthera tigris* home range size and prey abundance: Important metrics for management. *Fauna & Flora International, Oryx*, *48*, 370–377.

Simcharoen, S., Barlow, A. C., Simcharoen, A., & Smith, J. L. (2008). Home range size and daytime habitat selection of leopards in Huai Kha Khaeng wildlife sanctuary, Thailand. *Biological Conservation*, *141*, 2242–2250.

Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N., & Ericsson, G. (2012). From migration to nomadism: Movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, *22*, 2007–2020.

Terborgh, J., Lopez, L., Núñez, P., Rao, M., Shahabuddin, G., Orihuela, G., … Balbas, L. (2001). Ecological meltdown in predator-free forest fragments. *Science*, *294*(5548), 1923–1926.

Torres, N. M., De Marco Júnior, P., Santos, T., Silveira, L., de Almeida Jácomo, A. T., & Diniz-Filho, J. A. F. (2012). Can species distribution modelling provide estimates of population densities? A case study with jaguars in the neotropics. *Diversity and Distributions*, *18*, 615–627.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, *70*, 164–168.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Cruz C, Zarza H, Vidal-Mateo J, Urios V, Ceballos G. Top predator ecology and conservation: Lesson from jaguars in southeastern Mexico. *Conservation Science and Practice*. 2021;3:e328. https://doi.org/10.1111/csp2.328